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HITHERTO OVERLOOKED ANATOMICAL DATA CONCERNING THE GENITAL STRUCTURES IN THE RHOPALOCERA.

By B. C. S. Warren.

Manuscript received 19th March, 1957.

(Read 1st May, 1957).

With 3 Plates.

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I. Introduction.

This work was started as an investigation of the male genitalia of *Pyrgus serratulae* Rambur and the genital plate in the females of some *Pyrgus* species. The data acquired led to such an extended field of research that it has become impracticable to deal with the results as a whole; consequently the paper has been divided into the three sections which now follow.

II. On the Presence of a Subscaphium in *Pyrgus serratulae*, and the Origin and Evolution of the Vinculum in the Rhopalocera.

In the male genitalia of species of *Pyrgus* particular interest attaches to a pair of processes that were originally described by Reverdin as the "lateral apophyses of the uncus". Later he abbreviated this to "lateral apophyses", having doubts as to whether they had greater affinity to the dorsal or ventral elements of the structure. This uncertainty has continued ever since and the complex nature of these processes has remained unrecognised. Some time ago I noticed an abnormal appearance in these apophyses in an old photograph by Reverdin of *P. serratulae* and, on looking at my own mounts, noted the same feature, just visible, in some of them. This led me to make a fresh detailed examination of the apophyses of this species, and, incidentally, it testifies to the value of photography in illustrating genitalia, for no drawing would have

given any inkling of the presence of such an abnormality. My examination disclosed the remarkable fact that the two heads of the apophyses were connected internally by a strongly curved, sclerotised bridge, springing from the edges of the spines with which the heads are densely covered. This bridge is deeply embedded in the circumanal membrane, supporting it from below. It is seen from the ventral aspect (*i.e.* looking into the concave face) in Plate I, figure 7 ; and a lateral view showing the domed, dorsal curve of the bridge rising above the spined side parts of the apophyses is shown in figure 6 on the same Plate, on which the circumanal membrane is also faintly visible. This view can only be obtained by forcing the bridge slightly upwards so that the lower edge shows above the sides : in its normal position the dome of the bridge, deeply enclosed in the circumanal membrane, just surmounts the sides and appears indistinguishable from them.

As I had never observed a similar structure in any other species, I consulted the literature dealing with the scaphium, which seemed in some ways an analogous structure. The scaphium was dealt with in detail by Chapman (1911) in an article illustrated by two plates, one of photographs and the other of diagramatic figures but, as so often happens, the latter illustrates the views of the author rather than the appearance of the structure one may expect to find in nature. An obvious discrepancy between Chapman's diagrams and photographs led me to refer to a more recent article by Beirne (1942), whose observations and drawings agree with those of Chapman, and equally disagree with Chapman's photographs. I therefore examined the four European species of *Papilio*, for Gosse gave the name " scaphium " to the organ found in species of this genus. My mounts showed that the organ in the four European species was, unquestionably, similar to that shown in Chapman's photographs of three non-European species ; it does not agree in various respects with the descriptions and drawings given by these two writers. I quote from Beirne's work (1942 : 17) since it is the more recent :

> " The anus opens at the end of the abdomen at the end of a membraneous tube, the *anal tube*, which is occasionally sclerotized dorsally, this sclerotization being in the form of a long, narrow plate, known as the *scaphium*, the basal end of which is articulated with the ventral side of the uncus while the anus opens beneath its apical end."

Actually the scaphium in *Papilio*, in both the European and the foreign species shown in Chapman's photographs, is not a single, dorsal narrow plate, but a paired structure, comprising two dorsal processes more or less attached to the circumanal membrane, springing from two dorsal arms that are prolongations of a segment-like ring, clearly homologous to the vinculum (*see* Plate I, figs. 1–5). This ring, which is open dorsally but otherwise entire, is loosely articulated beneath the base of the uncus, and has complete freedom of movement under both the tegumen and uncus. It is in fact the genital segment, supporting the phallic organs and claspers, as can be seen in Plate I, figure 3 (*P. hospiton*) and figure 5 (*Iphiclides podalirius*). In the latter the aedeagus has been removed, but the connection of the claspers is obvious. When the claspers are in use this genital ring can assume an almost completely external position beneath the uncus ; but when not in use, it slides far back beneath, and inside, the tegumen. The complete freedom of action proves it to be an independent segment ;

it is neither the ninth, which is represented by the tegumen, nor the uncal segment. It can be removed intact from the other structures without damage to any of them (*see* Plate I, fig. 2, which shows the ring of *P. alexanor*). If further proof is needed, in *I. podalirius* all the dorsal structures of the genitalia are lost; there is no trace of either tegumen[1] or uncus, but the genital ring remains intact, holding the gigantic claspers and the phallic organs in position (Plate I, fig. 5). In all species the dorsal part of this ring is prolonged (bent over) into a more or less horizontal position, forming the two dorsal arms to which the sclerites of the scaphium are attached. There is a distinct difference in the structure of the fragments of the scaphium and that of their basal supports at the terminal point of the arms of the genital ring. The scaphium sclerites are thinner, more flexible, transparent, and more or less studded with minute spines or spikes, as can be seen in Plate I, figures 1, 4 and 8. This characteristic, as we shall show later, reappears in other families wherever sclerites that can be assumed to be of similar nature and origin are still extant. The scaphium sclerites differ markedly in different species; thus there is in *P. machaon* (Plate I, figs. 1 and 8) only one sclerite attaching to each arm, while in *P. hospiton* (Plate I, fig. 3) there are two, of which the distal pair are slightly rolled at their free edge and look as if they might at one time have been united, although now, as in all other species examined, they are distinctly separate. An idea of the extent of this separation is given in Plate I, figure 8, where the uncus and the ventral parts have been cut off to enable the specimen to be spread flat and viewed from above. Plate I, figure 4 shows the same view of *I. podalirius* and gives a good idea of the more symmetrical formation of the scaphium sclerites in this species. They are also more delicate and lie closer together than in the other species, but are still completely separate. The nature and origin of the scaphium sclerites of Gosse are now unmistakable; they do not articulate with the internal surface of the uncus or with any part of it; the processes that do so are those of the subuncus: this will be dealt with later. The question remains as to what is represented by the genital ring, and how it attained this strange position beneath the uncus and tegumen, but before considering this another point concerning the ring must first be noted. It will be seen in Plate I, figures 1–3 that two strongly sclerotised filaments hang down from varying points of the dorsal parts and connect with the dorsal angle of the base of the claspers (especially distinct in figs. 2 and 3, while in figure 1 the filaments are appended to the membrane below the dorsal bend of the ring). The ventral connection of the claspers is to the juxta, but the latter is supported by the ring. All these facts make it abundantly clear that this ring is a primitive type of vinculum. In the hope of obtaining further data I examined the European species of *Parnassius*. These display the usual type of vinculum as in the great majority of the Rhopalocera, which is remarkable considering the affinity of this genus to *Papilio*. In one species, *P. mnemosyne*, two short, narrow but strong rods spring from the internal surface of the uncus (Plate I, fig. 9); their purpose is obscure, but they are not in any way homologous to the scaphium of *Papilio*. They are far removed from the anal membrane and are connected only to the uncus. I have not as yet found such uncal rods in any other species of the Rhopalocera; it is possible that they exist in other

[1] This, of course, means that in this species the ninth abdominal segment has been completely lost.

eastern species of *Parnassius*. Chapman describes certain " appendages to the uncus " that occur in the Notodontids, but figured them (1911) as attached to the ventral edges of the uncus, giving them the name " subuncus ". Unfortunately some confusion has arisen as he figured them elsewhere diagramatically in the position of the brachia, an error very liable to occur in drawings that do not show actual objects, and unfortunately the mistake has been repeated by several recent writers who have not realised that the brachia do not spring from the uncus, but from the tergum of the uncal segment. I doubt if the subuncus in its exactly typical formation exists in the Rhopalocera, but it is probable that the strange uncal attachments existing in some Hesperiidae, for example in the genus *Nisoniades*, are homologous to them. In any case the rods in *P. mnemosyne* have no connection with the subuncus for, as noted, they are articulated to the internal surface of the uncus and do not come into contact with the edges. Having failed to obtain any further data concerning the genital segment from *Parnassius*, I turned to the genus *Zerynthia* (= *Thais*). This genus exhibits a primitive stage of structure that provides the desired information with a clarity and certainty such as is rarely obtainable when working on elaborate and complicated structures that have attained the considerable degree of uniformity developed in almost all the families of the Rhopalocera.

In *Zerynthia*, as represented by *Z. hypsiphyle* and *Z. rumina*, the ninth abdominal segment is not far from being a complete ring, dorsally broad and tapering to the sternum which, centrally, is membranous (*see* Plate II, figs. 11 and 16 ; in the latter the segment is separated and viewed from above, the ventral gap being seen through the tegumen). This formation is very remarkable, and unique so far as I know in the Rhopalocera, approaching as it does a united ninth segmental ring that does not possess any of the recognised attributes of the " vinculum ". The tenth segment follows in an almost embryonic normality, lying under the ninth tergum, and is of approximately equal circumference to the ninth segment, on a common axis with it. It also is nearly a complete ring, but the membranous gap is dorsal, between two expanded, roundish laterotergites. The phallic organs are contained in this segment and the claspers supported by it ; the sternum is somewhat expanded and bears two lateral flaps that extend baseward (*i.e.* proxad from the ring). All these features, clearly visible in Plate II figures 11, 13 and 14, prove that the tenth abdominal segment is the primeval genital segment in the Rhopalocera ; the sternal arc serves as the vinculum of recent times, and the two lateral flaps of the sternum are beyond doubt rudiments of the saccus of later origin. The genus *Papilio* gives confirmation of this, for in it the saccus is taking form, though sometimes no greater in depth than the flaps in *Zerynthia*, and united into a single process. The tergum of the eleventh segment is present, following the tenth, lying under its laterotergites and bridging the membranous gap between them. It is completely free from the tenth tergum under the distal area, but united to it at the extreme proximal edge. The uncus, consisting of two quite separate, somewhat rectangular, pointed processes, articulates to the distal rim of the eleventh tergum, and from the latter also extend two short and blunt, but strongly sclerotised, protrusions at each side of the uncal parts. These are rudiments of the brachia that become such specialised characteristics in the Satyridae, and all of which can be seen in the

photographs. In Plate II, figure 13 the ninth segment has been drawn slightly away from the tenth in mounting so that the ring of the latter can be seen, and in figure 11 the dorsal elements are visible in their natural position beneath the ninth tergum, and so is the narrow ring of the tenth between the sides of the ninth and the bases of the claspers, the latter having been drawn slightly away from the ring so that its exact dimensions can be recognised. As both claspers are in position, the left side of the ring of the tenth segment appears less distinct beneath the overlying parts. The aedeagus can be seen centrally, supported in the ring of the tenth segment. Owing to the proximal attachment of the eleventh and tenth terga it is not possible to separate these terga without breaking them but, as already noted, a large part of the dorsal area of both is quite free. No trace of the eleventh sternum remains. It is now obvious that the uncus is a part of the eleventh segment, not of the tenth, as has always been accepted. The claspers are connected by a membranous articulation to the ring of the tenth segment, but, at their dorsal corner, they connect with an extension of the eleventh tergum. This can be seen in Plate II, figure 13, as a dark bar extending from the collar of the eleventh tergum to the apex of the base of the clasper (most distinct on the left side). There is no trace of the juxta ; the ventral corners of the claspers curl slightly inward and rest side by side, their only attachment being to the ring of the tenth segment. The fact that the claspers are dorsally linked to the eleventh tergum, and no trace of the sternum remains, suggests that the juxta may be a remnant of the latter. Where it exists in *Papilio* it is supported at the distal face of the genital ring (see Plate I, figs. 1 and 3), which makes it unlikely that the juxta is a remnant of the ninth sternum.

The lines of evolution between the more primitive structures in *Zerynthia* and those in *Papilio* are not difficult to visualise, for some changes are already evident in the former. The ninth sternum, already incomplete, becomes further reduced, as also the tenth tergum, the tergum of the eleventh segment becoming connected through the increasing gap with the distal rim of the ninth tergum (tegumen). The tenth segmental ring sinks and becomes loosely articulated beneath the eleventh tergum and, having been forced off its axis, is able to assume an orientation approaching that familiar in the vinculum in its recent formation. The lateroventral flaps of the tenth sternum have already united and varying types of saccus are already present. This stage shows the primeval vinculum. The great freedom of action afforded to the genital segment by these changes is immediately obvious when compared with the embryonic position in *Zerynthia*. The Papilionidae are the only family that reveal these stages of development ; but it is interesting to note that the genital segment in the specialised genus *Parnassius* has attained the advanced stage established throughout the Rhopalocera, in spite of the many primitive characteristics appertaining to the genus. How did this further advance take place? The primeval vinculum (or primary vinculum as I shall call it), which might almost be said to constitute a free-moving internal segment, is the basic support of all the genital organs, which fact is of the utmost importance. The tenth segment was, and in spite of its changed position still is, the genital segment. How was it discarded and its functions passed to a greatly diminished ninth segment? The recognition of the true nature of the primary vinculum as the tenth segment, and of the changes that enabled its freedom from segmental

alignment to be arrived at, provide the answer. The dorsal reduction and ventral displacement of the primary vinculum have continued, always doubtless in order to obtain the necessary freedom, range of action and protection for the claspers, which were almost negligible when the genital segment was held in a constant position, as in *Zerynthia*. The ring of the primary vinculum became divided somewhere above the level of the top of the claspers, the dorsal arms remaining isolated. These tergites subsequently became attached to the lower edges of the tegumen, while the ventral arc of the ring became attached to its proximal edge in place of the long lost sternal portion, a junction that automatically made possible the retraction of the claspers to far within the eighth segment. This union of the sternal elements of the tenth and the dorsal element of the ninth segments is evidenced unmistakably by the fact that the point of junction is still almost always distinctly visible, often indicated by a sharp angle, or sudden change in width between the dorsal and ventral parts of the ring, while in many species the actual junction is a membranous articulation. This is especially marked in many Argynninae where, at the junction, the parts are freely movable, a fact that has been recorded previously (Shirôzu and Yamamoto, 1953). Such, doubtless, was the sequence of events that led to the combination of vinculum and tegumen as a unit in the position it now occupies in the majority of families. But, judging by Drosihn's work (1933), in some genera of Pieridae (*Colias*, and possibly others) the same result has been attained in a different way. The tegumen has been reduced almost to vanishing point, and the appearance of the primary vinculum suggests that it has been able to rise from beneath the receding tegumen until level with it, then becoming attached to its proximal end. In this way one can assume that the narrow, complete ring of the primitive tenth segment has actually occupied the original site of the ninth, the latter being reduced to a mere tergal arch, lying between the tergum of the tenth segment and the base of the uncus. Confirmation of this change can be seen in the junction of the dorsal corners of the claspers with the eleventh tergum by an appended filament (as in *Zerynthia*), while the ventral corners attach to the sternum of the tenth ring (also as in *Zerynthia*); yet the tenth tergum is separated from the eleventh by the tergum of another segment, which can only be the ninth. In the earlier stage the tenth and eleventh terga must be in contact, and would still be so in these Pieridae if the ninth and tenth segments had not changed places. In other Pieridae (such as *Aporia*), the more usual partition of the primary vinculum is shown to have taken place by the presence of isolated rudiments of the dorsal parts of the ring attaching to the sides of the tegumen between the vinculum and uncus. Such tergites left by the severance of the primary vinculum assume a very great variety of formations and methods of attachment to the edges of the tegumen along which they run. They appear hanging loosely in a membranous surround, or closely articulated, when they are practically united with the tegumen and form a thickened edge, as seen in Plate II, figures 15 and 20. In some cases they are attached at one end only; these I call "hanging" tergites, for they are movably articulated to the tegumen, but hang free as in figure 12. A good idea of the great variety of shapes these tergites can assume in the Argynninae is given by numerous photographs in my earlier works (Warren, 1944 and 1955). These tergites have been referred to as rudiments of the brachia, or as extensions of the lateral edges of the uncus, either of which

would suggest they are derivatives of the eleventh tergum. But their undoubted homology with the dorsal arms of the primary vinculum is seen in the fact that occasionally the sides of the vinculum (tenth sternum) extend some way distad from the point of junction with the tegumen, and are then abruptly broken off. Such free-standing ends, continuous with the vinculum ring, result from the severance of the dorsal ends. They are sometimes very conspicuous in the Lycaenidae (*see* Bethune-Baker, 1914, fig. 10). Again, in many cases, a thin filament from the proximal end of the tergites connects with the dorsal corner of the claspers (*see* Plate II, fig. 20), just as in *Papilio* such a filament connects the clasper and ring, while the latter is still complete (Plate I, figs. 1–3). Yet again, the dorsal arms of the complete ring in *Papilio* occupy the same positions relative to the tegumen and uncus and display the same degrees of orientation as do the isolated tergites. Such facts leave no real doubt as to the nature and origin of these fragments ; but it is noteworthy that the tergites never agree in shape or dimensions with those parts of the uncus to which they are nearest (*see* Plate I, fig. 10). This is a clear indication that the two approximating parts never constituted one whole that has become divided, for had they done so the parts in proximity would show some degree of similarity in size or formation at the point of partition.

While the tenth segment was undergoing such extensive metamorphosis, the ninth was also greatly affected ; the establishment of the primary vinculum in the position of the original ninth sternum was only the climax of these changes. The ninth sternum had disappeared by the time the primary vinculum had attained its freedom of internal movement. It is certain, therefore, that any process based on the existing sternal parts of the ninth segment must be of secondary origin, that is it developed after the primary vinculum and ninth tergum became connected. Remarkable examples of such developments are the vanni, present in many species of the Argynninae. In some species of *Issoria* they are rudimentary, in others they have united into a single plate ; in *Fabriciana* they have attained the maximum development possible (*see* Warren 1944, fig. 18). I may add that much of what I then wrote (1944) on these vanni is incorrect, because of my supposition that they were products of the gnathos. To return to the scaphium, we now know that the supports to which its sclerites are attached in *Papilio* are the dorsal arms of the primary vinculum (tenth segment) ; the uncus, below which the scaphium lies, we know to be the eleventh tergum. It follows, therefore, that the sclerites constituting the scaphium must be remnants of the twelfth abdominal segment, for nothing the least resembling these sclerites existed when the tenth segment was still in its original position. Viewed in this light, the nature of the lateral apophyses and the sclerite that connects them in *Pyrgus serratulae* becomes apparent. They are compound structures; the fixed supports spring from the distal edges of the tegumen and are certainly extensions of the isolated tergites of the primary vinculum, for the latter has attained its recent position in the Hesperiidae. The suture separating the thickened edge of the tegumen from its main body is easily seen in most specimens, as also is the membranous gap that separates the sides of the uncus at its base from the tegumen (*see* Plate I, fig. 6 and Plate III, fig. 40), which shows that the connection has been a secondary one after the original junction of the uncus (eleventh segment) with the dorsal edge of the tegumen (ninth segment). The spinous heads of the apophyses,

common to all species of *Pyrgus* belonging to the subgenus *Ateleomorpha*, are below the anal membrane, but in some cases their uppermost spines become connected with it, as in *P. serratulae*. The bridge that connects the heads in the latter species, springing from their internal edges, is deeply embedded in the anal membrane, which it supports from below. This sclerite is therefore the subscaphium of Pierce, the counterpart of the scaphium and unquestionably of the same nature and origin. So far as is known, this subscaphium in *P. serratulae* is unique in the Rhopalocera. It differs from the scaphium in being attached transversely to the anal membrane and in being a single piece. The unusual nature of the spined, curved heads, their position and partial attachment to the anal membrane and connection with the sternite of the twelfth segment, all suggest that they are also derivatives of the twelfth segment.

In one or two other species of *Ateleomorpha* one finds minute fragments that may be remnants of a subscaphium at the base of the heads, but in only one case, *P. schansiensis*, are they of such proportions as to make this certain. In this species two strips with spined edges rise, internally, from the heads on each side of the anal membrane, and more or less connect with it (Plate II, fig. 15). They certainly constitute lateral, though not ventral, supports to it. Their composition is more that of the heads than of the subscaphium, but they are further evidence of the common origin of both heads and subscaphium. The homology of these fixed apophyses in all sections of the genus *Pyrgus* is obvious, in spite of some differences of development. In the subgenus *Pyrgus* (the section I described as the *Hemiteleomorpha*) the dorsal, strongly curving processes (Plate III, figs. 30, 33 and 36), are similar in nature to the spined heads in *Ateleomorpha*, but they are united ventrally by a filament that passes well below the anal membrane, and bears a ventral sclerite of similar nature to those composing the scaphium in *Papilio*—a further indication that these apophyses are remnants of the twelfth segment. Of the four species of this subgenus, *P. malvoides* has developed apophyses of a different type (Plate III, fig. 38). The supports are broad prolongations of the tenth tergites, expanding in width to their extremities as do those of the subgenus *Scelotrix* (*Teleomorpha* Warren) (Plate III, fig. 40). The elongated, curving, spined processes of the other three species are wanting. In the species of the subgenus *Scelotrix* the expanding ends of the supporting tergites are joined by a ventral plate of the type of sclerotisation seen in the scaphium, though the spines that cover it are a little stronger. This plate, and the distinct difference in structure between it and the supports to which it is attached, are clearly shown in Plate III, figure 40. These facts leave little doubt that, like the other sclerites of the apophyses, this plate is a remnant of the twelfth segment, the actual sternum, for it is well below the anal membrane. In the past, like all writers, I referred to apophyses of this type as the "ring of the tenth segment", which we now know is impossible. All the lateral apophyses in *Pyrgus* are homologous, but in *Scelotrix* they differ in being broadly united by the ventral plate. The wide supports cause the process to appear more ventral than in the other two subgenera, so I shall distinguish them under the name of "subapophyses". All types of these apophyses are fixed and immovable; they are known only in the genus *Pyrgus*. A sternal plate of similar structure exists in some species of *Issoria* (Argynninae), but these differ from the apophyses of *Pyrgus* in having a membranous attachment and being freely movable.

Another process frequently confused with the lateral apophyses is the gnathos of Chapman (1911). When writing Chapman took this to be the " tenth abdominal sternite ", noting its presence in many Nymphalidae. This process is a development of the hanging type of tergite of the primary vinculum, consisting usually of two narrow arms, movably articulated to the tegumen at their base, as shown in Plate II, figure 12. These arms connect with the membrane of the genital cavity, which is often widely but weakly sclerotised, uniting the arms at their extremities. The extent of sclerotisation of the membrane varies considerably, and rarely produces any true sclerite, for it passes imperceptibly into non-sclerotised membrane. In a few cases a filament connects the edges of the arms and the base of the uncus. This, as in the cognate case of the vanni, must be a secondary development ; it also appears in some *Issoria*.

In the Rhopalocera little remains of the eleventh segment beyond the uncus and brachia. In the most primitive type known (that in *Zerynthia*) the uncus, extremely small in comparison to the claspers, consists of two somewhat triangular parts that lie close together but are not united. They are movably articulated to the base of the tergum. This is very distinct from the ordinary type of bifid uncus ; I know only two European species, apart from *Zerynthia*, in which the uncus still consists of two completely separate parts, *Parnassius mnemosyne* and *Pyrgus malvae* (Plate I, fig. 9 and Plate III, fig. 30). The brachia of Muschamp (1915) must also be mentioned as, like the uncus, they have always been considered developments of the tenth segment. They are an integral part of the eleventh tergum, developed on each side of the uncus. In *Zerynthia* one sees the most rudimentary form, two small excrescences on each side of the uncus (Plate II, figs. 13 and 14), in the Satyridae the most specialised. Beirne suggests that they are identical with the socii of the lower Lepidoptera, possibly derived from the anal prolegs of the tenth segment of the larva. But, as noted, the brachia are an integral part of the eleventh tergum, so could not be homologous with the anal prolegs of the tenth sternum : any such process would have to be situated below the anus, not above it. I doubt if the socii exist in the Rhopalocera, having never seen any process that would seem to correspond with them.

The following is a list of the structures that have been discussed, with a brief note on the nature of each as demonstrated by the data given. The names are used in the sense in which they were originally applied.

Tegumen : the tergum of the ninth abdominal segment.

Genital segment : the tenth abdominal segment, supporting the phallic organs, juxta and claspers.

Primary vinculum : the ring of the tenth abdominal segment, freed from segmental alignment, carrying the phallic organs, juxta and claspers with it.

Vinculum : the sternal arc of the tenth abdominal segment (the genital arc) connected to the tegumen, either fixed or movable.

Uncus : tergal process of the eleventh abdominal segment.

Subuncus (Chapman) : paired appendages attached to the edges of the uncus ; unusual in the Rhopalocera : not to be confused with the uncal rods of *Parnassius mnemosyne* that are attached to the internal surface of the uncus.

Brachia (Muschamp): lateral extensions of the tergum of the eleventh abdominal segment, of which they are an integral part. Most frequent and specialised in the Satyridae; rudimentary in *Zerynthia*.

Scaphium (Gosse): paired laterodorsal sclerites of the twelfth abdominal segment, attached, dorsally, to the anal membrane, and connecting with the dorsal arms of the primary vinculum.

Subscaphium (Pierce): sclerite of twelfth abdominal segment attached to under surface of anal membrane, supported (in the Rhopalocera) by fixed lateral apophyses. As yet known only in *Pyrgus serratulae*.

Lateral apophyses (Reverdin): compound structures, paired extensions of tergites of primary vinculum, immovable, supporting sclerites of twelfth abdominal segment; separate, or connected ventrally by filament (genus *Pyrgus*).

Subapophyses: compound structures, immovable extensions of primary vinculum united by sternite of twelfth abdominal segment (genus *Pyrgus*).

Gnathos (Chapman): hanging tergites of primary vinculum, movably articulated to tegumen, connecting at their extremities with membrane of genital cavity that is more or less sclerotised.

Juxta: ventral sclerite of uncertain origin; supported by primary vinculum in *Papilio*.

It is emphasised that the data given apply only to the Rhopalocera; they may apply to the Heterocera also, but to establish this would need much further research. It is possible that they indicate a different line of evolution in the Rhopalocera. It should be noted that certain structures known by similar names in the Rhopalocera and Heterocera may not be homologous.

It has been shown that in one family (Papilionidae) the genital segment, that is the tenth abdominal segment, exists in three different positions: (1) as an almost complete segment in embryological alignment between the ninth and eleventh segments, (2) as a free-moving, internal, segmental ring; and (3) disunited into isolated parts that connect with parts of the ninth abdominal segment. Within one family such stages must indicate degrees of development, not separate lines of evolution. The last, as the most remote from the primeval segment, must be the most recent. In all other families only this recent stage exists—conclusive proof of the primitive nature of the Papilionidae. The metamorphosis through which the tenth abdominal segment has passed had, so far as can be seen, the sole object of increasing the freedom, and extending the range of movement and protection of the claspers. To this end the dorsal elements of three segments have undergone incessant changes, sometimes to the extent of complete obliteration, while the claspers continue to develop. It is noteworthy that even in the smallest species the claspers still remain the most prominent feature and the fundamental and vital nature of their function is therefore proved beyond all question. In systematic work characters of most other elements must be regarded as of secondary importance, unless in agreement with those of the claspers.

III. On the Evolution of the Western Race of *Pyrgus malvae*.

It has often been stated that the genital plate of the eighth sternum of the female of *Pyrgus malvae* is divided into two parts in European forms but

united in Asiatic forms. Further, it has been said that if this plate is completely united it then becomes indistinguishable from that found in *P. malvoides*. This plate in some families is so unstable that its use as a specific character is not justified; but in *Pyrgus*, though variable, it retains in most species characteristics that will distinguish them. It therefore seemed useful to make a detailed examination of the Asiatic insects, with a view to establishing the nature of such variation as the plate exhibited. I use the name "genital plate" to cover the entire structure and its many developments: it only becomes confusing to apply separate names to various parts of such a variable structure. I started by examining specimens from Korea, the extreme limit of the easterly range of the species. This gave me, in both sexes, structures that at first sight seemed to differ more from western *P. malvae* than many other species of *Pyrgus* differ from each other. *P. malvae* is extremely specialised, and in structure the male differs totally from the other species of the subgenus in the formation of the uncus, lateral apophyses, claspers and style and stylifer. Three of these specialised formations are unique in the genus. The genital plate in the female is also distinctive. On closer study these structures in the Korean insects are found to be, fundamentally, precisely those that distinguish *P. malvae*, though in each part the development is such that they differ recognisably but without losing their specific characteristics. A verbal description of these characters could apply to either insect. On recognising this, my first thought was to find out if these eastern and western types overlapped at all within their wide range. It soon became apparent that, in fact, this did occur and the light thus thrown on the anatomical nature of European *P. malvae* is worth recording. In the first place the Korean insect must be distinguished by a name; so I describe it below as:

Pyrgus malvae subsp. **coreanus** subsp. n.

Superficially subsp. *coreanus* differs little from subsp. *malvae*: the white spots on the underside of the hind wings are sometimes considerably restricted, making the brownish ground colour more evident; but considerable variation occurs. Anatomically the two races differ unmistakably: in *P. malvae* the entire male genitalia are reduced in length and increased in depth (Plate III, fig. 30 shows typical subsp. *malvae* formation; fig. 36 that of subsp. *coreanus*). This change in relative proportions affects every part of the organs. The uncus in each is of the same primitive type, such as has been shown (p. 369) to exist in *Zerynthia*, *i.e.*, composed of two totally separate roughly triangular parts, movably articulated to the small band that remains of the eleventh tergum, which in turn is joined to the tegumen. These parts, though broader in subsp. *malvae*, are the same length in both races, but are set more obliquely to the central line of the tergum in *malvae*, which renders it impossible for them to lie (or be caused to lie) parallel when the genitalia are mounted in profile. In subsp. *coreanus* the articulation of these two parts of the uncus is at right-angles to the tergum. This can be seen in Plate III, figure 36 as an almost straight, dark line; as a result the parts lie parallel quite naturally, as seen in the figure. Viewed from above, however, they are seen to stand apart in a V-formation, as in *malvae*. Their line of articulation in the latter is not straight, but roughly angled, a point projecting baseward from its centre. In the female of *coreanus* the genital plate is both longer and broader and is entire, the neck of the bursa is strongly sclerotised, especially the ventral edge which extends through the opening in the plate (Plate II, fig. 23). In *malvae* the neck of the bursa is normally membranous, and the plate divided into two parts (fig. 22).

Holotype male, allotype female, two male and three female paratypes, all from Hakugan, Korea.

The most important feature in these races is the development of the uncal parts. The double process, each part independently articulated to the tergum is, as we have seen, a primitive type. The method of articulation in *coreanus* shows how the usual (recent) type of uncus could have originated. If figure 36 in Plate III is compared with figure 38, the similarity is obvious. The latter shows the uncus in *P. malvoides*, which is semi-united, the parts being joined basally but separated distally. Figure 39 on the same plate shows this uncus from below and it can be seen that the dividing line between the two parts runs about half way up from the extremity, while near the tip the separation becomes increasingly pronounced. Plate II, figure 17, shows the tip highly magnified, the parts stand apart and then touch again at the extremity, but neither here nor at the extreme base of the dividing line are they actually united. Such an uncus is a clear demonstration of how the two-piece process became a united uncus. The *coreanus* type, therefore, links the more primitive and the semi-united types, but the *malvae* type could not lead to the semi-united because the two parts of the uncus are divergent. In this respect it is a deviation from the *coreanus* type, which must have been the original form ; European *malvae* has therefore been evolved from this eastern race.

P. malvae coreanus occurs in various parts of Korea ; I have specimens from three localities. Beyond Korea it extends into the Sikhota Alin range in the Maritime Province, the most easterly as well as northerly locality from which I have seen specimens. I have none from Manchuria, but in Amur a female shows the first variation : the neck of the bursa is not sclerotised. It may be well to note at this point some details of the female genital plate. The formation in normal European *malvae* is as in Plate II, figure 22, which shows the plate divided into two parts. At the basal (proximal) end it is recurved, appearing as two black ends in the photograph. About half way up on the external edge of each part the line of sclerotisation is broken by a membranous gap, which in the photograph has the appearance of a small excision in the margin. In *coreanus* (fig. 23) the basal recurved edge is seen to extend completely across the base, but is not so broad as in *malvae* : the membranous gap in the sides is also obvious. Plate II, figure 21 shows the normal plate in *P. malvoides*, where the basal recurved end is confined to the central third of the base, the outer third on each side being membranous. The line of sclerotisation of the sides is not broken. These characters are constant in both species; whatever the extent to which the two parts of the plate in *malvae* may unite, it can never be mistaken for the *malvoides* plate, as has been suggested. In the other two species of the subgenus, *P. melotis* and *P. pontica* (Plate II, figs. 18 and 19), the characters of the plates are so obvious as to need no describing. But it is important to note that *P. malvae* differs from the other three species in having the opening of the bursa in the centre of the genital plate, whether this is entire or in two parts, whereas in the other species the opening is before the plate ; proxad to it. In the figures of *melotis* and *pontica* this is very obvious, the strongly sclerotised edge of the neck of the bursa just connecting with the proximal end of the plate. In *malvoides* (Plate II, fig. 21), the neck of the bursa has been detached in mounting the specimen, but it is situated immediately below the recurved end of the plate, and the two thin, black lines seen one on each side of the latter are broken off edges of the neck. This is another characteristic that renders the *malvae* plate unmistakable.

These points noted, the changes in the development of the *coreanus* characteristics as one passes westwards may now be considered. Leaving Amur, and passing into Transbaikalia, variation becomes the rule. Westwards from the Yablonoi Mountains (the Apfelgebirge in all German publications of the last century), at high or low levels, the genital plate deviates markedly towards the *malvae* type, appearing in numerous forms of which Plate II, figure 24 is a good example: one specimen was actually typical of *malvae*, as in figure 22. In the males the same variation exists, each process tending towards the *malvae* type, even to the extent of a transitional form of uncal articulation, in which the two parts stand more obliquely, though still far from the extreme type. Still further west, in Irkutsk, the same changes are taking place, well illustrated in Plate III, figure 33, which shows the apophyses of the *malvae* type, the combined style and stylifer a perfect transition, and the uncus still of the *coreanus* type. In the great mountain ranges to the south, the Kurai Mountains and Western Altai still give transitional forms, but specimens also occur completely typical of *malvae* in both sexes. The example from the Ongodai district (Plate III, fig. 30) is typical of European *malvae* in every detail; some females are the same but transitional specimens occur. From a little further south-east Elwes obtained normal *malvae*, and from much further south in the Tian-Shan I also have normal *malvae*. There is no means of estimating the proportion of intermediates over this vast area: one can only say that the available data suggest that Transbaikalia and Irkutsk are the area of least stability. From the Altai to the Tian-Shan typical *malvae* is apparently more frequent and typical *coreanus* seems not to have persisted far west in Amur. It is certain, however, that once *malvae* extended west of the great mountain chains of Central Asia, the *malvae* characteristics had developed to their ultimate limit. All change ceases. The changes in altitude, latitude or longitude encountered between the east coast of Asia and the central ranges were no greater than those to which *malvae* was subjected in its further passage to the extreme west, but it never deviates again in the slightest degree from the established type. It is obvious that outside influences, ecological or otherwise, can have played little, if any, part in the development of this type. Some idea of its constancy is afforded by the fact that specimens from England, Greece, Lapland, the Altai or the Pamirs cannot be distinguished anatomically. The immense period of time throughout which this constancy has persisted indicates how improbable is the idea that *P. malvoides* can have developed from *P. malvae*. Further, we have already shown that the *malvoides* type of uncus could not originate from the *malvae* type, though it might from the *coreanus* type. But *malvoides* is, and has been for centuries, completely separated from the latter by *malvae*: so that the possibility of *malvoides* being specifically linked to *malvae* through *coreanus* is ruled out. The formation of the apophyses, so markedly different in *malvoides*, suggests that it has originated from some entirely independent source. I know of no other case in which the evolution of a race can be traced with such certainty by a closely-linked chain of still living forms, from one distinct type in the extreme eastern limits of the Palaearctic Region to another in the extreme western. The immense period of time during which the compound race has persisted in Central Asia, for it must be of far greater antiquity than the western *malvae*, is no less remarkable than the constancy of the latter once it became established. The facts prove that *malvae* came to

Europe from the east and developed on the way, but it must be emphasised that it is a development of one and the same strain as *coreanus*.

An approach to this unique case is seen in the racial variation of *Pyrgus alveus*. Of this species, the race described by Kauffmann (1954) as subsp. *colurnus* shows a range of anatomical variation linking that shown by the eastern subsp. *iliensis* Rev. with the extreme development seen in European *P. alveus* subsp. *alveus*, which is not, so far as I can ascertain, constant anywhere. The *alveus* and *colurnus* types occur together throughout the central Alps, though in differing proportions, and the transition from one to the other is imperceptible. Even in those southern regions where *colurnus* predominates, the extremely developed *alveus* type also occurs. In this case the European Alps are the area in which the evolutionary changes are taking place. In time the extreme type of *alveus* structure may become stabilised, as with *malvae*, but at present the structural formation is closely linked to the size of the individual specimen : the smaller the insect the more frequent the reduced *colurnus* type of structure. The valuable data collected by Kauffmann provide us with a link between European *alveus* and the Asiatic race *iliensis*. The degree of constancy the latter has attained, its westward range, and the extent to which it may develop structural characteristics approaching the *alveus* formation, cannot be judged owing to lack of material.

IV. On the Taxonomic Value of Certain Corrugant Sclerotisation Affecting the Sternum of the Eighth Abdominal Segment in Females of the Subgenus *Scelotrix* (Genus *Pyrgus*).

The details given in the last section on the female genital plate led me to hope that in the subgenus *Scelotrix* (= *Teleomorpha* Warren) this plate would prove an equally reliable guide to speciation. To a certain extent this proved to be the case, but the differences are slight and variation renders them difficult to observe. When working on these species it became apparent that the curious, corrugant sclerotisation that affects a large part of the eighth sternum showed remarkable characters, distinctly linked to speciation. For example, Plate III, figures 25 and 28 show the well-known species *Pyrgus cacaliae* and figure 29 the closely related *P. andromedae*. It will be seen that the curious, heavy lines of corrugation in *P. cacaliae* run more or less transversely across the segment, while in *P. andromedae* they are wavy and few in number, running in a somewhat less distinctly transverse direction. The difference in this segmental sclerotisation between the two is far more obvious than any difference in the form of the small genital plate which lies distad to the corrugation. The variation in the plate in the two figures of *P. cacaliae* is noticeable, that in Plate III, figure 28, being somewhat similar to that in figure 29 (*P. andromedae*). Another striking form of the corrugation is seen in *P. carthami* (fig. 27), the one species in the European section of the subgenus in which the genital plate is really strikingly distinct. In these three species, however, it would be quite impossible to fail to recognise the segmental corrugation at a glance.

For many years the specific nature of the insect I described as *Pyrgus freija* has been in doubt. It has been held by many writers to be a race of *P. centaureae*. I have found it impossible to reconcile many of the statements made with the facts known to me. Recently I had an opportunity to examine a really good series of specimens from Canada and this showed *P. freija* to be

a very variable insect. I was also able to dissect several females. These mounts proved beyond doubt that *P. freija* and *P. centaureae* were distinct species, and also explained much of the past uncertainty. To make absolutely certain I obtained further female specimens from localities in Scandinavia and North America from which I had not previously seen specimens, and I have now dissected specimens from 14 localities in North America, ranging from Colorado north to Churchill and Newfoundland, and including both *freija* and *wyandot*. The result leaves no doubt that *P. centaureae* does not exist in North America : those workers who stated that *freija* and *centaureae* were the same species were only comparing two races of *freija* : the latter and *wyandot*. I have often described the male genitalia of *freija* and *centaureae* (of Europe and Asia) and reference to the female structure will now simplify the question. Plate III, figures 35 and 37 are of Scandinavian *P. centaureae*. The corrugation is seen to be weak and to run on the sclerotised edges of the sternum, an extended area of the latter being membranous. In *freija* (fig. 31, a specimen supposed to come from Lapland), the corrugation is marked and of the *cacaliae* type. Figure 34 (a specimen from Alberta) is of the same type. In figure 32 (*P. wyandot* from New Jersey) the corrugation is of the *freija* type but somewhat finer. In all three examples the genital plate is of the same type as in *P. centaureae*, but smaller. The variation between *wyandot* and *freija* is of the same nature as occurs in *P. cacaliae* (figs. 25 and 28) and also in *P. andromedae*. There is no question that *freija* and *centaureae* are distinct species ; these characters of the segmental sclerotisation in the female confirm those known to exist in the male. *P. wyandot* will, of course, become the specific name. As already stated, the variation in *freija* is marked and many specimens come close to *wyandot* : the form known as *loki* is only a form of *freija* with heavier white spots. In my work on these females I came on one specimen from the collection of the late Dr. Chapman bearing a label in his handwriting " Lapland, Staudinger " which I take to mean that the specimen was one brought back by Staudinger on the occasion of his collecting trip to Lapland (Plate III, fig. 31). I have also dissected my type female of *freija*, supposed to come from Lapland, and the mount was very much the same as Plate III, figure 34. The question whether *freija* really does occur in Europe still remains to be solved, but I feel sure there can be no mistake about the Staudinger specimen. The variation that occurs in *freija* may be one of the reasons why it has not yet been recognised, but against this we can now set the fact that, anatomically, the females can be identified at a glance. There may well be poor female specimens in collections that have been passed over as *P. centaureae*.

These results led me to turn again to the still more obscure question of *P. sibirica* Rev. and Chapman's specimens which I had named *P. chapmani*. Very few specimens of either are known and the chance of getting more extremely remote. On dissecting my female of *chapmani* I was pleased to find the corrugations were very distinctive, and also that the intersegmental membrane between the seventh and eighth segments was broadly, though weakly, sclerotised, showing strong corrugations which curved centrally towards the seventh segment. On applying to the Geneva Natural History Museum, however, it transpired that Reverdin's series contained only one female, the type, which could not be dissected. Fortunately I had a note that Dr. Verity, some 25 years before, had obtained from Bang-Haas the remaining specimens of the series from which

Reverdin's type specimens had come, and among them was a female which he very kindly allowed me to dissect. This gave me a mount identical to that of my specimen of *chapmani* (Plate III, fig. 26), which, considering the very specialised nature of the corrugations, shows the two are the same species. The slight differences in the male genitalia must be individual variations, the few specimens dissected being insufficient to demonstrate this. Another important question has also been settled by these two female specimens. Some writers have referred to *P. sibirica* as a race of *P. centaureae*, presumably because of the slight nature of the differences in the male genitalia, but this was not justified. Nevertheless such an extreme difference in the segmental structure of the females was scarcely to be expected (compare Plate III, figs. 35 and 37 with fig. 26). It may be recalled that both *P. centaureae* and *P. sibirica* are known to occur in the Altai mountains and, though only two specimens of the female of the latter have been dissected, the existence of the *sibirica* type so far to the east in the Sajan Mountains (the locality of *chapmani*) proves it not to be just an abnormality.

There can be no doubt that this remarkable segmental sclerotisation, apparently restricted to the subgenus *Scelotrix*, is of specific importance. The genital plate is also of value, and can be distinctive as in *P. carthami* (Plate III, fig. 27), but in other cases, as previously noted, its value is obscured by variation, and characterisation is so slight as to be unrecognisable except by comparison of two examples simultaneously, or of two photographs taken to a known magnification, as on the accompanying plates. It may be of interest to add that in *P. sidae* the corrugations exist only in the intersegmental membrane, where they appear as extremely fine lines in the membrane, which is otherwise unsclerotised. The males of this subgenus are characterised by the presence of the sternal plate of the twelfth segment, which testifies to their primitive nature; the females are no less remarkably characterised by the segmental corrugation, which confirms the isolated nature of the subgenus.

V. Acknowledgments.

I have to express my thanks for much help in obtaining material necessary to the completion of this paper. I am especially indebted to Professor Teiso Esaki for the gift of specimens from Korea, a district from which little is ever available; to Dr. Ch. Ferrière for permission to dissect a male paratype of *Pyrgus sibirica* Rev. from the Geneva Natural History Museum; to the authorities of the British Museum (Natural History) for material from a number of Asiatic localities and to Mr. T. G. Howarth for help in searching for specimens from specified localities; to the authorities of the American Museum of Natural History and Mr. Cyril F. dos Passos for the gift and loan of North American specimens; to Dr. Roger Verity for permission to dissect a specimen from the original series of *Pyrgus sibirica*; and to Mr. M. Opheim for arranging for the loan of specimens from the Tromsö Museum.

VI. Summary.

1. A general re-examination of the genitalia of certain species of *Pyrgus* and other Papilonidae, and their comparison with other Rhopalocera, has shown that the primary vinculum is the tenth abdominal segment, which is the primeval genital segment, and that the uncus is part of the eleventh segment and not of the tenth, as has always been accepted.

2. The development of this in the Papilionidae, from the primeval condition in *Zerynthia* to the advanced stage in *Parnassius*, which is the same as is found throughout the Rhopalocera, is discussed in detail and the combination of the vinculum and tegmen as a unit is described with illustrations from the Argynninae and the Pieridae.

3. The effects of this metamorphosis on the ninth segment are also discussed and the scaphium is identified as a remnant of the twelfth segment, as is also the subscaphium of Pierce. The gnathos of Chapman is shown to belong to the primary vinculum, and the brachia of Muschamp to the eleventh segment. These and other terms are described succinctly on p. 369.

4. The great value of photographs instead of diagrams for studies such as this is emphasised.

5. Study of the genitalia of specimens of *Pyrgus malvae* from the various portions of its wide range has shown that, although those from the extreme east appear strikingly different from the western forms, the fundamental plan is so essentially similar, and there are so many connecting forms from the intermediate areas, that the extreme eastern form which is here described, can only be regarded as the primeval race of the species. The relationships with *P. malvoides* are discussed and the linking of this species to *P. malvae* through *coreanus* is regarded as improbable.

6. The case of *P. malvae* is compared with that of *P. alveus*, which, however, is shown to be somewhat different.

7. Extension of this investigation to the subgenus of *Pyrgus*, *Scelotrix*, has revealed a new diagnostic character peculiar to this subgenus in the corrugated sclerotization affecting a large part of the eighth segment, and this has shown clearly that *P. freija*, though quite distinct from *P. centaureae*, which does not occur in North America, is a race of *P. wyandot*. This character also serves to show that *P. sibirica* is a species quite distinct from *P. centaureae*.

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PLATES I–III.

All figures are × 18, unless otherwise mentioned. All photographs by the author.

PLATE I.

FIG. 1.—*Papilio machaon*; primary vinculum with scaphium, in natural position, underneath, and between the sides of both tegumen and uncus.

FIG. 2.—*Papilio alexanor*; primary vinculum with scaphium, showing filamentary appendages that connect with the claspers.

FIG. 3.—*Papilio hospiton*; primary vinculum with scaphium, drawn from beneath tegumen; right clasper attached to filament and juxta; left clasper removed.

FIG. 4.—*Iphiclides podalirius*; dorsal view of scaphium.

FIG. 5.—*Iphiclides podalirius*; primary vinculum, scaphium and claspers. Note absence of tegumen and uncus.

FIG. 6.—*Pyrgus serratulae*; complete genitalia, showing dome of subscaphium extending above lateral apophyses.

FIG. 7.—*Pyrgus serratulae*; concave aspect of subscaphium, seen between the lateral apophyses from below.

FIG. 8.—*Papilio machaon*; dorsal view of scaphium; uncus cut off.

FIG. 9.—*Parnassius mnemosyne*; uncal rods seen projecting from beneath the two points of the uncus.

FIG. 10.—*Fabriciana niobe gigantea* Stg.; uncus and part of tegumen, showing dorsal tergites of primary vinculum attached by membrane to edges of tegumen.

PLATE II.

FIG. 11.—*Zerynthia hypsipyle*; complete genitalia, lateral view, showing ring of tenth abdominal segment in normal position.

FIG. 12.—*Liminitis populi*; genitalia with ventral organs removed, showing gnathos (hanging tergites of primary vinculum).

FIG. 13.—*Zerynthia hypsipyle*; dorsal view of tenth abdominal segment showing membranous, dorsal gap, with tergum of eleventh segment, uncus and rudiments of brachia showing beneath it.

FIG. 14.—*Zerynthia hypsipyle*; tenth abdominal segment, with tergal area of eleventh segment attached, seen from above showing the expanded dorsal tergites and intervening membranous gap; also the two ventral extensions. Note the complete separation of the two parts of the uncus, with point of aedeagus seen below them.

FIG. 15.—*Pyrgus schansiensis*; dorsal structures, showing lateral apophyses bearing sclerites of twelfth abdominal tergum.

FIG. 16.—*Zerynthia hypsipyle*; ninth abdominal segment, showing small ventral gap, seen from above through the tegumen. (Compare with fig. 11, which shows profile view of the tapering sides).

FIG. 17.—*Pyrgus malvoides*; distal extremity of uncus, × 270.

FIG. 18.—*Pyrgus melotis*; genital plate of female.

FIG. 19.—*Pyrgus pontica*; genital plate of female.

FIG. 20.—*Clossiana selene*; dorsal structure, showing tegumen with tergites of primary vinculum attached, from which filamentary appendages connect with base of clasper.

FIG. 21.—*Pyrgus malvoides*; genital plate of female.

FIG. 22.—*Pyrgus malvae*; genital plate of female.

FIG. 23.—*Pyrgus malvae coreanus*; genital plate of female.

FIG. 24.—*Pyrgus malvae*; genital plate of female transitional between *malvae* and *coreanus*, from the Yablonoi Mountains.

PLATE III.

FIG. 25.—*Pyrgus cacaliae* ; sternum of eighth abdominal segment of female.

FIG. 26.—*Pyrgus sibirica* ; sternum of eighth abdominal segment of female.

FIG. 27.—*Pyrgus carthami* ; sternum of eighth abdominal segment of female.

FIG. 28.—*Pyrgus cacaliae* ; sternum of eighth abdominal segment of female.

FIG. 29.—*Pyrgus andromedae* ; sternum of eighth abdominal segment of female.

FIG. 30.—*Pyrgus malvae* ; male genitalia, left clasper removed. Ongodai, Altai.

FIG. 31.—*Pyrgus wyandot freija* ; sternum of eighth abdominal segment of female. Lapland.

FIG 32.—*Pyrgus wyandot* ; sternum of eighth abdominal segment of female.

FIG. 33.—*Pyrgus malvae—coreanus* ; complete genitalia, male. Transitional specimen from Irkut.

FIG. 34.—*Pyrgus wyandot freija* ; sternum of eighth abdominal segment of female. Alberta.

FIG. 35.—*Pyrgus centaureae* ; sternum of eighth abdominal segment of female. Odalen, Norway.

FIG. 36.—*Pyrgus malvae coreanus* ; complete male genitalia. Hakugan, Korea.

FIG. 37.—*Pyrgus centaureae* ; sternum of eighth abdominal segment of female. Saeterstoen, Norway.

FIG. 38.—*Pyrgus malvoides* ; dorsal structures of male genitalia.

FIG. 39.—*Pyrgus malvoides* ; uncus × 85.

FIG. 40.—*Pyrgus carthami* ; dorsal structures of male genitalia, showing the subapophyses. Note the difference of sclerotisation between the tergites of the primary vinculum and the sternite of the twelfth abdominal segment which they support.

Genital structures in the Rhopalocera.

B. C. S. Warren.

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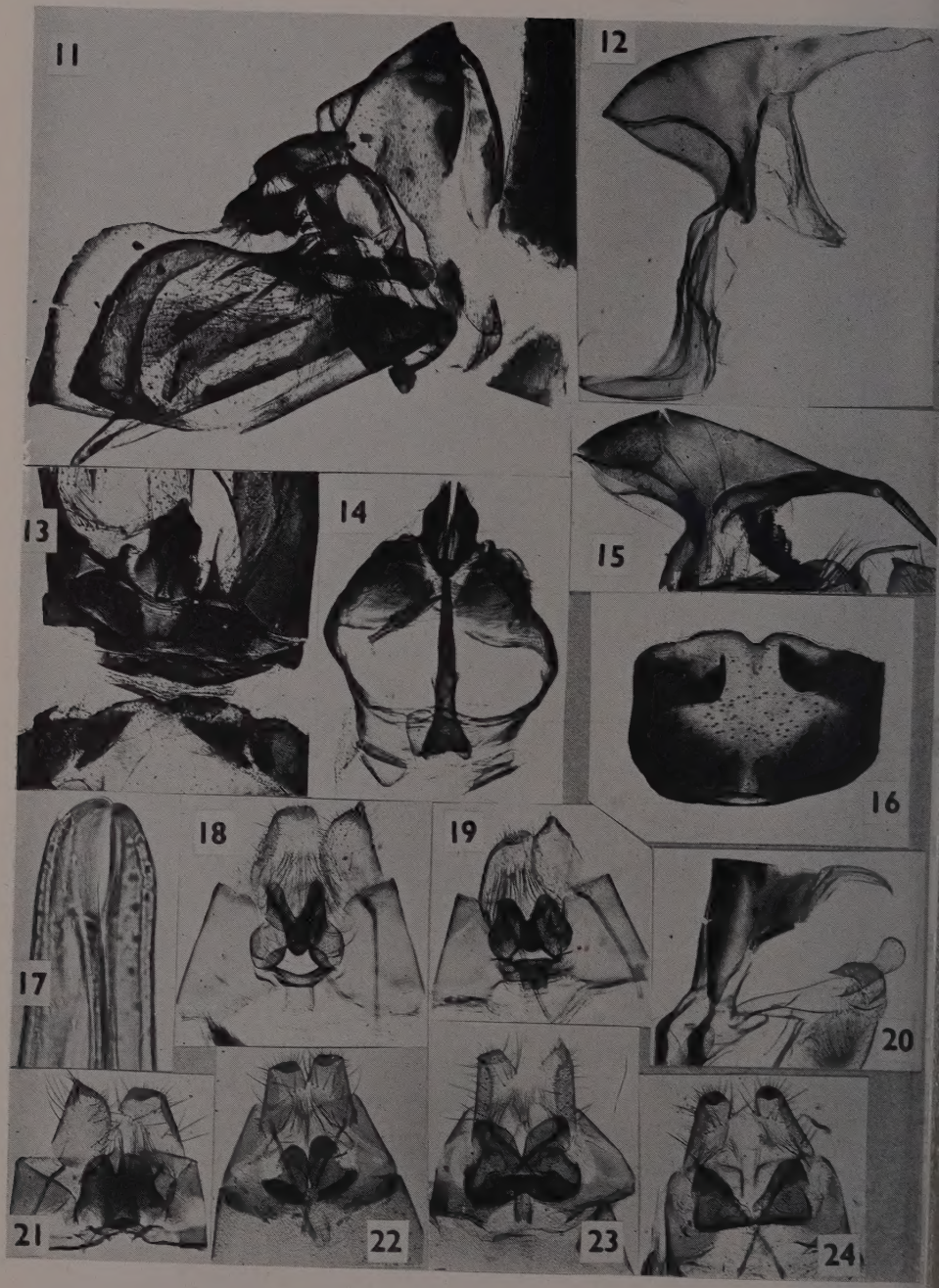

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